

NOTES ON SEASONALITY AND HABITAT ASSOCIATIONS OF
TROPICAL CICADAS (HOMOPTERA: CICADIDAE) IN
PREMONTANE AND MONTANE TROPICAL MOIST
FORESTS IN COSTA RICA

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Abstract—Annual patterns of adult emergences and habitat associations for several species of tropical cicadas (Homoptera: Cicadidae) were studied within the premontane-to-montane tropical moist forest zone northwesterly of the Meseta Centrale region of Costa Rica. The region largely consists of expansive coffee plantations, secondary vegetation, and strips of forest along streams, and the censusing of cicadas at four widely separated localities (Grecia, Naranjo, San Ramon, and Esparta) covered an elevational range of about 200–1,100 meters. Coffee plantations in this region have an overstory (shade cover) of *Inga* spp. trees (Leguminosae) and sometimes (Grecia) a mixture of these trees with another legume tree, *Zygia longifolia*. *Z. longifolia* is also the dominant tree in forest remnants along streams in this region. Given the pronounced patterns of annual seasonal precipitation at all four localities and the mosaic of secondary coffee plantations and forest remnants at three of them, and forest remnants and secondary vegetation at the fourth (Esparta), it was expected that the census of nymphal skins and adult cicadas would indicate distinctive seasonal adult emergence cycles and habitat associations. The data confirmed this. *Fidicina amoena* emerges during the dry season near stream-edge *Zygia* trees in coffee plantations (Grecia) and near other legume trees in forest remnants (Esparta). *Fidicina semilata* and *F. "coffea"* emerge near *Inga* trees in coffee plantations (Naranjo and San Ramon) during the dry season as does *F. pronoe* and *F. spinocosta* in secondary vegetation (Esparta). *Fidicina mannifera* emerges during the wet season in primary forest remnants at about 200 meters elevation (Esparta). *Zammara smaragdula* emerges in the wet season near *Zygia* trees in coffee plantations (Grecia) and forest remnants along streams (Naranjo and San Ramon) and *Conibosa* sp. emerges during the wet season in coffee plantations (Grecia, Naranjo, and San Ramon). *Quesada gigas* emerges during the dry season near *Zygia* trees along the borders of coffee plantations and in stream-edge forest remnants. The data are discussed from the standpoint of adaptations in tropical cicadas to seasonality and habitats, the latter particularly in terms of the exploitation of legume trees as feeding sites (root crowns) of nymphs.

Introduction

A field survey of the cicadas across northern Costa Rica, extending from lowland tropical wet forest into montane wet forest, montane moist forest

and into lowland tropical dry forest, revealed distinctive distributional patterns for many genera and species (Young 1976). Such a transect slices through a series of distinctive climatic and vegetation zones (Holdridge et al. 1971) and varying degrees of seasonality in terms of the length and severeness of the dry season (Janzen 1967). Several previous studies have revealed that tropical cicadas may exhibit very pronounced adult seasonal emergences annually, and that genera and species sometimes also partition the local environment by habitat (Young 1972, 1974, 1975, 1980a, b, 1981a). These studies were conducted for the common genera and species found in these regions of Costa Rica: lowland tropical wet forest, premontane tropical wet forest, highland moist forest, and lowland tropical dry forest. The purpose of the present paper is to summarize the annual peak adult emergence periods and habitat associations for several genera and species of tropical cicadas in yet another major climatic belt of northern Costa Rica, the premontane-to-montane tropical moist forest zone. The data, although discontinuous, indicate that some cicadas of this zone emerge during the lengthy dry season, others during the wet season, and that most species are differentially associated with (a) forest remnants forming the borders of coffee plantations and grazing pastures, (b) shade trees in coffee plantations, and (c) secondary vegetation. The data are consistent with observations on cicada emergences at other sites in Costa Rica in that emergences are strikingly seasonal, and that a variety of habitats, including agricultural ones, are exploited by cicadas in the tropics.

Materials and Methods

I examined the temporal and spatial properties of adult emergences of cicadas by selecting four widely separated localities along the northwest axis through the highlands and adjacent mountains northwest of the Meseta Centrale region of Costa Rica: habitats located at the cities of Rosario de Grecia (Grecia), Naranjo, San Ramon, and Esparta, sites within Alajuela and Puntarenas Provinces (Fig. 1). This transect covers an elevational gradient from 825 meters (Grecia), 1042 meters (Naranjo), 1116 meters (San Ramon) down to 208 meters (Esparta). The first three localities are very similar topographically and floristically, consisting of rolling hills covered with extensive coffee plantations at least 100 years old in most parts, and with strips or remnants of forest vegetation along streams and rivers (Figs. 2, 3, 4). The coffee plantations have an overstory of primarily *Inga* spp. trees (Leguminosae) (Figs. 2, 3) and the forest remnants consist chiefly of adult-size *Zygia longifolia* trees (Leguminosae) (Fig. 4). The coffee plantation at Rosario de Grecia consisted of adult-size *Zygia* trees along streams and drainage ditches running through the plantings, and *Inga* trees as shade on slopes. Patches of grasslands are interspersed with the coffee agricultural



Fig. 1. The distribution of localities within the premontane-to-montane tropical moist forest zone in Costa Rica, northwest of the Meseta Centrale and San Jose, used to study cicada emergences. These localities are: (1) Grecia, (2) Naranjo, (3) San Ramon, and (4) Esparta.

system of the region. The fourth site, Esparta, is a very steep (incline about 60° in most places) forested ravine surrounded by patches of secondary growth and open pastures lightly to heavily grazed by Brahma cattle (Fig. 5). In this forest bordering a stream system, several genera of legume trees predominate, of which *Pithecollobium* species predominates. A marked dry season, of similar duration and severeness, is a major component of the climatic regime of all four sites (Fig. 6). Areas within each habitat studied at each locality are representative of the habitats in general.

A cicada census program was deployed at these four localities to test the hypothesis that representative cicada species at each one exhibit distinct annual emergence patterns somehow related to the annual seasonal cycle of precipitation (Fig. 6). A second hypothesis examined, also in a preliminary fashion, was that cicada emergences occur in different kinds of habitats at each locality, habitats that are representative of each locality overall. As with previous similar studies (Young 1972, 1974, 1975, 1980a, b, 1981a) cicada emergence patterns were studied by making collections of freshly



Fig. 2. The overstory of *Inga* spp. trees in the coffee plantation at Naranjo where emergences of *Fidicina semilata* and *Conibosa* sp. were studied. These shade trees, easily recognizable by the whitish bark, are rather uniformly distributed over large areas of the plantations in this locality.

discarded nymphal skins from marked plots in different habitats at each locality. The skins were collected, identified in the field to species, sexed, and counted every time a census was made. Whenever possible, adult specimens were also collected for voucher material to confirm species determinations later. Sample plots for collecting nymphal skins were usually 5×6 meters and in coffee plantations, about half were enclosing one *Inga* shade tree and the others only coffee bushes. Plots with shade trees also have coffee bushes, and the DBH for the shade trees is 20–35 cm. Nymphal skins were collected exhaustively from tree trunks, bushes, leaf litter, and ground surface. For most species, skins are readily identified to species based on gross morphological features (size, form, coloration). The reliability of species determinations of skins in this manner has been discussed elsewhere (Young 1980a). Because skins remaining from a previous year's emergence period are very discolored, broken, and crumbly, they are readily distinguished from fresh skins of the current emergence thereby eliminating a bias



Fig. 3. *Inga* spp. shade trees interspersed with coffee bushes in a plantation at San Ramon. Cicada nymphal skins were collected from the ground litter, coffee bushes, and trunks of shade trees, and special care was taken to examine branches cut away as part of pruning of coffee bushes as shown here.

of confusing two or more annual emergence periods. Records were also kept for adult cicadas heard or seen at times when nymphal skins were censused.

For the Rosario de Grecia locality the study plots were situated within two areas of a large coffee plantation, the selection of the plots being based on previous observations of nymphal skins in them. Prior visits to all four localities indicated that at least two large-bodied species of cicadas were active at each one. The Grecia coffee plantation has a mixed shade cover of *Z. longifolia* and *Inga* spp. trees, while the Naranjo and San Ramon plantations have several species of *Inga* trees as shade. In addition to setting up sample plots in coffee in Naranjo and San Ramon, I also established a large study plot along a forest remnant in San Ramon, adjacent to a coffee plantation. *Z. longifolia* is the only tree species in this plot. At Esparta, cicada nymphal skin distributions were examined by selecting plots around some adult-size legume trees where skins had been seen. Details of the sizes



Fig. 4. Stream-edge habitat near San Ramon showing a large *Zygia longifolia* tree (on right bank of stream), a typical emergence spot for cicadas such as *Zammaria smaragdula*.

of plots, total areas represented by sample sites, and census dates are summarized along with the data. The census program spanned a period of about two years and included samples taken in both wet and dry seasons.

Because my samples of nymphal skins are very discontinuous over each year of the study, one source of error in estimating density of emerging cicadas from my census program is the possibility that some nymphal skins were blown into the plots from other areas of the habitats studied, although more than 80% of the skins collected from all plots throughout the study were found attached to vegetation. Unlike some temperate zone cicadas, clean emergence holes are not commonly found in tropical species.

Results

The cicadas associated with each locality are shown in Figures 7 and 8 and can be described further as follows:

(A) GRECIA: *Fidicina amoena* ● medium to large-bodied cicada (body



Fig. 5. An overview of the canopy of the primary forest remnant in the steep ravines at Esparta during the dry season. There are also surrounding patches of secondary vegetation in addition to pastures. The sides of the ravines with forest are steep (45–60°).

length 30 mm), greenish body all over, clear wings, bell-like chirp for courtship song. Also found at Naranjo, San Ramon, and Esparta, although not abundant. Common in some parts of the Meseta Centrale (Young 1980a), but not common in lowland and premontane tropical rain forest (Young 1972, 1980b). Probably scarce in lowland tropical dry forest, although a population occurs at Santa Rosa National Park (Young 1981a).

Zammara smaragdula ● medium-sized cicada (body length 25 mm), distinctly mottled green and black body all over, bright green in male, more olive green in female; wings clear but with large black spots; “hoarse buzz” for courtship song. Also found at other localities mentioned above for *F. amoena* but excluding tropical rain forest sites in the northeast where it is replaced by *Z. smaragdina*; also found at Finca La Taboga, near Canas in lowland Guanacaste Province as well as at the Barranca Forest site (Young 1981a).

Quesada gigas ● large-bodied cicada (44 mm), body all over streaked in shades of brown, olive green, and black; clear wings; very distinctive “lo-

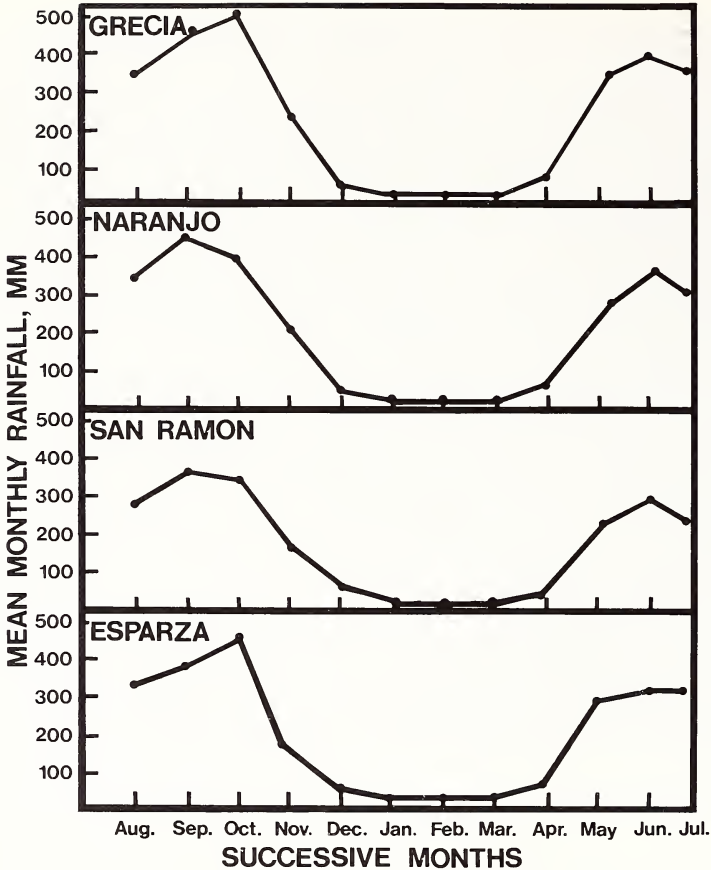


Fig. 6. The distribution of precipitation at the four localities within the premontane-to-montane tropical moist forest zone, showing a distinct and similar dry season between December and April for all localities. Data are means for the period 1943–1973. The standard deviations and coefficients of variation for monthly mean values are strikingly similar among all four localities, as expected for the very similar mean values for each month among all localities. Data is courtesy of the Meteorology Service of Costa Rica.

comotive whistle"-like courtship song, sometimes sings at dusk as do the others mentioned here but to lesser degree; widely-distributed throughout Costa Rica (Young 1976, 1980a, b).

Conibosa sp. • small-bodied cicada (10 mm) not figured in this paper, but with greenish head and thorax and maroon-colored abdomen and clear wings; courtship song resembles "zzzst" repeated over and over; widely distributed in the Meseta Centrale north of San Jose, and through the three coffee-growing localities discussed in this paper (see also Young 1980a), but not found to my knowledge in lowland to premontane tropical wet and dry

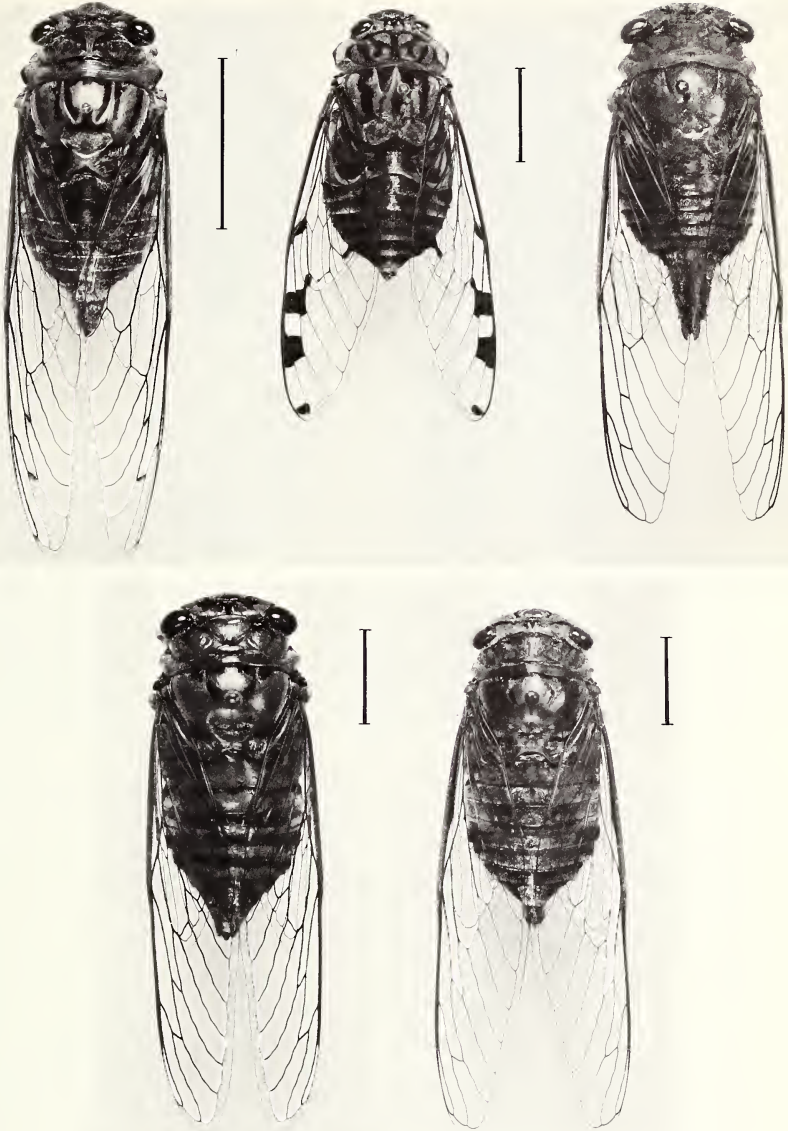


Fig. 7. Cicadas from the montane tropical moist forest zone in Costa Rica, northwest of the Meseta Centrale. Top row, left to right: *Quesada gigas*, *Zammara smaragdula*, and *Fidicina amoena*, three of the four common cicadas associated with predominantly coffee \times *Zygia* tree plantations in the Meseta Centrale, and lower montane moist forest region adjacent to it; Bottom row, left to right: *Fidicina semilata* and *Fidicina "coffea,"* two of three common cicadas associated primarily with coffee \times *Inga* tree plantations in the upper montane moist forest region. It both series, the cicada not shown is the small *Conibosa* sp., but it is figured in Young (1980a).

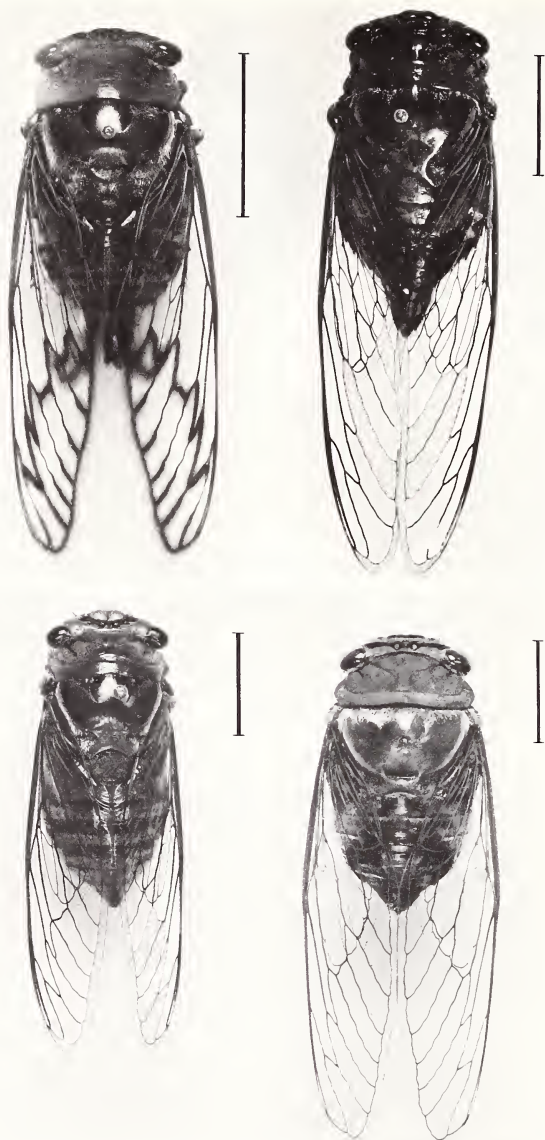


Fig. 8. Cicadas from the premontane tropical moist forest zone in Costa Rica, northwest of the Meseta Centrale. Top row, left to right: *Fidicina mannifera* and *Fidicina sericans*, two of four common primary forest species. Bottom, left to right: *Fidicina pronoe* and *Fidicina spinocosta*, the two common species associated with certain types of secondary vegetation in this region. The third common primary forest species of this region is *Zammara smaragdula*, figured in Fig. 7. For both Fig. 7 and 8, the vertical black line to the right of each cicada shown gives the actual body length relative to the magnified figure. See text for actual body length measures.

forest sites in Costa Rica. Appears to be distinctly associated with coffee plantations, perhaps more so than other cicadas.

(B) NARANJO: *Fidicina semilata* • species determination tentative as it may be a new species also tentatively called *F. "guayabana"* by A. M. Young and T. E. Moore; medium-sized cicada (body length 22 mm) with body generally greenish all over and wings crystal-clear; monotonous buzz-like courtship song and sings in coffee bushes and shade trees in coffee plantations; as to my knowledge found only at San Ramon in Costa Rica in addition to Naranjo.

(C) SAN RAMON: *Fidicina "coffea"* • probably a new species, tentatively determined by A. M. Young and T. E. Moore; medium-sized cicada (body length 23 mm), greenish but with some mottling (faint and thin) in brown, similar to *F. semilata* but with very distinctive courtship song consisting of pulsating buzz from coffee bushes and shade trees in plantations; not collected from other localities in Costa Rica; along with *F. semilata* appears somewhat restricted to the coffee habitat between Naranjo and San Ramon. May occur at Naranjo but not found.

(D) ESPARTA: *Fidicina mannifera* • large-bodied cicada (42 mm body length), dark brown with some mottling in green, particularly on prothorax dorsum; wings clear but with somewhat diffuse brown tinges along veins; very distinctive strong pulsating buzz, particularly at dusk; sings from trunks of large forest trees; widely distributed in northern Costa Rica outside of the Meseta Centrale and adjacent foothills (see Young 1972, 1976, 1980a, b).

Fidicina pronoe • medium-sized cicada (body length 25 mm) with cocoa-brown meso- and meta-thoracic dorsum and greenish head and prothoracic dorsum and lateral borders of meso- and meta-thoracic dorsum lined with white; wings clear and abdomen thickly banded laterally with black and brown; courtship song a high pulsating whistle heard mostly in open secondary vegetation where the canopy height is less than 7 meters; widely-distributed across northern Costa Rica (Young 1976, 1980b) and probably occurring at at least Naranjo and Grecia localities in the present study although most likely patchy and scarce as it is in the Meseta Centrale (Young 1980a). Probably not found in most localities in lowland tropical dry forest in Costa Rica but perhaps in Santa Rosa National Park (Young 1981a).

Fidicina spinocosta • at lower end of medium-sized range (body length 20 mm), body with head and thoracic areas bright green and abdomen maroon with silvery pubescence; body short and thick relative to other *Fidicinas* and wing length; wings crystal clear; courtship song is strongly pulsating short whistles mostly at dusk and from thick secondary vegetation; to my knowledge only occurs at this locality and also in the premontane tropical wet forest zone in the northeast (Young 1980a).

Fidicina sericans • large-bodied cicada (body length 30 mm) with black

Table 1. Notes on the seasonal distribution of adult cicadas along a transect through the Cordillera Central northwest of San Jose, San Jose Province, Costa Rica.

	Localities* where heard/ seen	Dry season dates areas examined	Wet season dates areas examined	Season of highest activity	Adult habitats	Habitats of nymphal skins
<i>Fidicina amoena</i>	RG, N, E	RG: II-12, 13; III-8; IV-16; V-10, 1973	RG: VII-21, 23; VIII- 20, 1973; VIII-29-74	dry	river-edge forest remnants, shade trees in coffee plantations	same
<i>F. semilata**</i>	N, SR	N: XII-29-31, 1972; I-11; II-11, 12; IV- 17, 27-28, 1973	N: VII-27-73	dry	shade trees in coffee plantations	same
<i>F. coffea**</i>	N, SR	SR: I-6-9; II-7-8, 1973	SR: VII-27-73; VII- 13-74	dry	shade trees in coffee plantations	same
<i>F. pronoe</i> and <i>F. spino- costa</i>	E	E: I-10; II-22; III-3, 17-19; IV-14-1973	E: VII-6-7, 13, 1974	dry (late)	secondary growth trees on hills; river-edge forest	same
<i>F. sericans</i>	E	Total dry season dates: 20	Total wet season dates: 7	dry	river-edge forest remnants in ravines	same
<i>F. mannifera</i>	E			wet	river-edge forest remnants in ravines	same
<i>Zannara smaragdula</i>	RG, N, SR, E			wet	river-edge forest remnants	same
<i>Quesada gigas</i>	RG, N, E			dry (late)	river-edge forest remnants	same
<i>Conibosa</i> sp.	RG, N, SR			wet	shade trees and cof- fee bushes in coffee plantations	
<i>Pacarina</i> sp.	SR, E			dry	open fields and young secondary growth	same

* The localities examined are: Rosaria de Grecia (RG), Naranjo (N), Esparta (E), San Ramon (SR).

** Species designations unconfirmed due to lack of information on genus *Fidicina* in general. *Fidicina semilata* is also coded as *F. "guayabana"* in MPM and UWMZ Collections, and *F. "coffea"* is a temporary designation.

body mottled with dark green; wings slightly smokey with tinges of brown; courtship song a steady buzz; associated with primary and advanced secondary wet to moist forest habitats in northeast premontane, lower montane, and lowlands with nymphal skins invariably found near adult-size canopy legume tree species (Young 1972, 1980b, unpublished).

Another small-bodied cicada, *Pacarina* spp., also occurs at Esparta and perhaps at San Ramon, where they are associated with grassland habitats (Young 1974) but these species were not studied here. A summary of the distributions, localities, habitats or adult cicadas and nymphal skins, are given for these species in Table 1.

As shown in Table 1, forms such as *F. amoena*, *F. "coffea,"* *F. semilata* *F. sericans*, and *F. pronoe* are active in the dry season at their respective localities and many of these species occur in coffee plantations and other disturbed habitats. *Z. smaragdula* is the common wet season cicada at several localities and it is associated with forest remnants, places where its nymphal skins are found beneath *Zygia* trees. There is considerable overlap for some species of *Fidicina* (those associated with coffee plantations) among several coffee-growing localities and *Z. smaragdula* is found at all localities studied (Table 2). Forest-associated *Fidicinas* are restricted to Esparta (Table 2). Although the data on emergences are discontinuous, peak numbers of nymphal skins for several species censused agree with seasonal activity patterns as seen from adults (Fig. 9). Densities of nymphal skins generally fall well below one nymphal skin per square meter, although censuses of the same species at different sites within a locality generate great differences in estimates of density (Table 3). In coffee plantations at Naranjo and San Ramon, the greatest abundances of nymphal skins of *F. semilata* and *F. "coffea"* occur in plots with *Inga* spp. shade trees (one tree per plot) and plots with only coffee bushes beyond the immediate vicinity of shade trees disclose few skins (Table 4).

Density estimates for cicada nymphal skins will be very sensitive to areas involved, particularly when data from two or more sites are polled when individual sample sizes are low. Yet for a species such as *F. semilata*, the low estimate of about 0.12 nymphal skins per square meter may be biologically significant as suggested by the rather continuous data on nymphal skins of this cicada obtained from a small patch of coffee (840 m²) within the city of Naranjo for the period 30 December 1972 through 28 April 1973, a time span covering the major portion of the emergence period of this species at this locality. A total of 97 fresh skins were collected from this coffee patch, which contained a living (freshly-cut) stump of an *Inga* tree (DBH-25 cm) and about 50 coffee bushes giving a density estimate of about 0.12 skins per square meter. More than 70% of the skins collected were located within a 3-meter radius of the tree stump. The wood of the stump was still fresh and green as the tree had been cut down about a month before my census was commenced.

Table 2. The distribution of cicada species in the Central Cordillera northwest of San Jose, in Costa Rica, based on records of adults and nymphal skins.

Cicada	Localities			
	Rosaria de Grecia (coffee farms)	Naranjo (coffee farms)	San Ramon (coffee farms)	Esparta (forested ravines: second growth)
<i>Zammara smaragdula</i>	+	+	+	+
<i>Quesada gigas</i>	+	?	?	+
<i>Conibosa</i> sp.	+	+	+	
<i>Fidicina amoena</i>	+	+	+	
<i>F. semilata</i>	+	+	+	
<i>F. "coffea"</i>		+	+	
<i>F. pronoe</i>				+
<i>F. spinocosta</i>				+
<i>F. mannifera</i>				+
<i>F. sericans</i>				+
<i>Pacarina</i> sp.			+	+

There is some evidence of habitat partitioning at Rosaria de Grecia in terms of cicadas associated with *Zygia* trees: *F. amoena*, *Z. smaragdula*, and *Q. gigas* all emerge near these trees but not at other trees used as shade here. Furthermore, *Z. smaragdula* exhibits a tendency to emerge close to streams: of 174 nymphal skins of this cicada collected on 23 July 1973 along five parallel rows of coffee bushes running along a stream bordered with

Table 3. Abundance and densities of nymphal skins of cicadas from study plots at several localities in the Central Cordillera of Costa Rica (1973).

Cicada species	Localities studied	Habitat studied	Total area examined	Number of sites	Densities of nymphal skins
<i>Fidicina amoena</i>	Rosaria de Grecia	coffee plantation	2,030 m ²	2	0.17, 0.27/m ²
<i>Fidicina semilata</i>	Naranjo	coffee plantation	1,256 m ²	2	0.12, 0.40/m ²
	San Ramon	coffee plantation; riveredge forest remnant	1,128 m ²	2	0.12, 0.28/m ²
<i>Fidicina "coffea"</i>	San Ramon	coffee plantation; riveredge forest remnant	1,128 m ²	2	0.08, 0.28/m ²
<i>Zammara smaragdula</i>	Rosario de Grecia	coffee plantation	2,030 m ²	2	0.30, 0.42/m ²
<i>Conibosa</i> sp.	Rosario de Grecia	coffee plantation	2,030 m ²	2	0.06, 1.61/m ²
	San Ramon	coffee plantation; riveredge forest remnant	688 m ²	2	0.41, 0.78/m ²

Table 4. Collections* of nymphal skins of *Fidicina* spp. cicadas proximal and distal to *Inga* spp. shade trees in coffee plantations at Naranjo and San Ramon in the central highlands of Costa Rica northwest of the Meseta Centrale.

No. <i>Inga</i> trees** censused	DBH range	Tree trunks	Range trunk	Coffee bushes within 16 m ² area (proximal)	Coffee bushes beyond 16 m ² area (distal)	Ground (<i>Inga</i> trees + coffee)	Total nymphal skins			
							oo	oo	T	
Naranjo: <i>Fidicina semilata</i>										
26	25–35 cm	35	0–12	108	5	12	93	67	160	
San Ramon: <i>Fidicina semilata</i>										
33	25–35 cm	23	0–2	127	8	11	87	59	146	
<i>Fidicina</i> “ <i>coffea</i> ”										
33	25–35 cm	16	0–2	23	2	10	22	19	41	

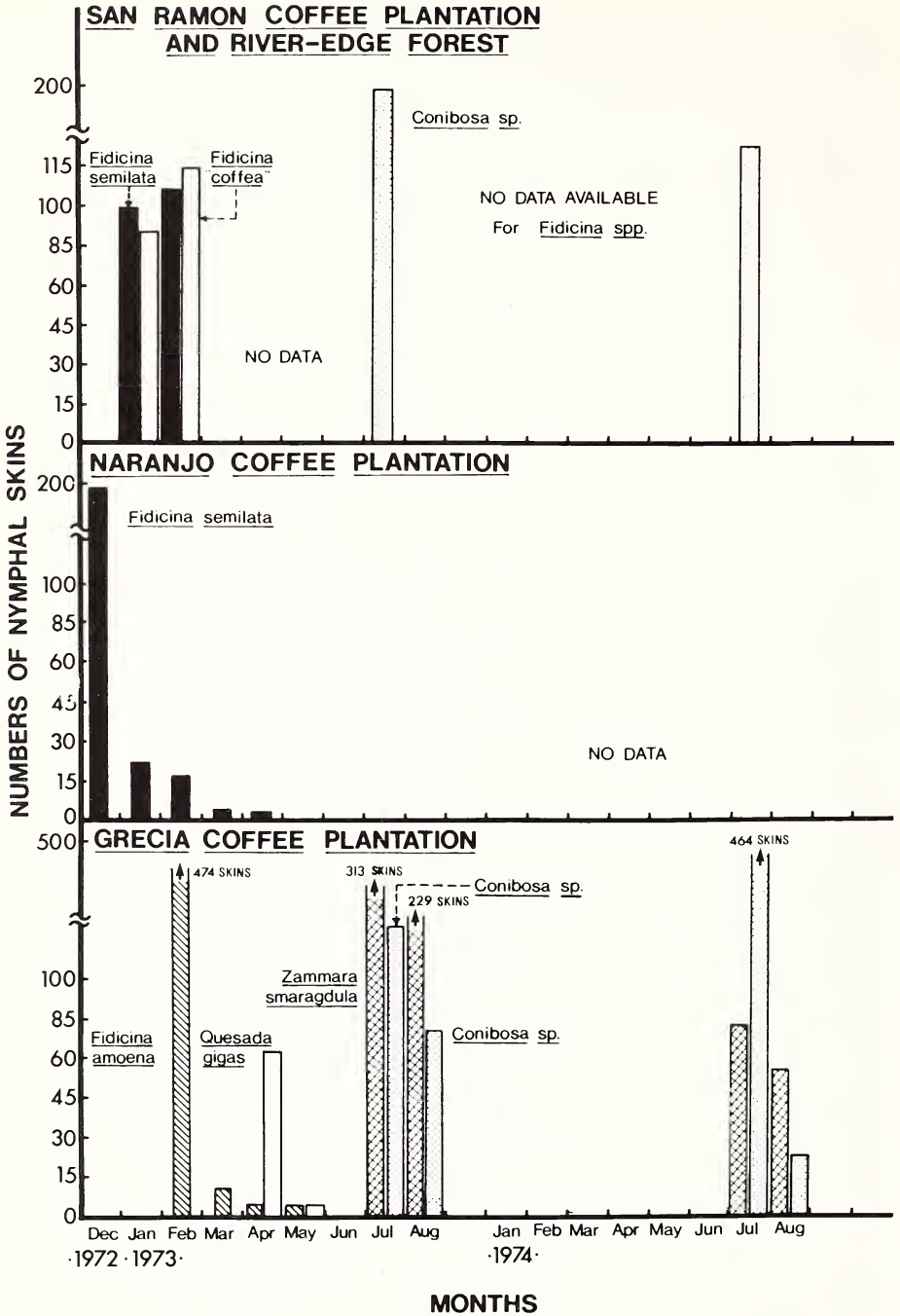
* Over 60% of the shade trees sampled were *I. aff. fissionalyx* and the remaining ones were *I. goldmannii* and *I. leptoloba*.

** Census dates for Naranjo: 29 December 1972, 11 February 1973, 17 & 28 April 1973; census dates for San Ramon: 6–9 January 1973, 7 February 1973.

Zygia, 100 skins were taken from the row of bushes nearest to the stream, and with a marked decline in other rows, with none being found in the fourth and fifth rows away from the stream. In areas of coffee at Grecia where *Inga* trees are mixed with *Zygia* for shade, nymphal skins of *Q. gigas* are found beneath both kinds of trees.

In one stream-edge plot (600 m²) containing six large *Zygia* trees and 25 coffee bushes on a steep incline of about 50°, two census dates (6 January and 7 February 1973) disclosed 69 fresh skins of *F. semilata* and 100 fresh skins of *F. “coffea”* with the distributions of the skins of the two species mixed within the plot but not measured. These data and the accompanying estimates of density (0.12 for *semilata* and 0.28 for “*coffea*”) suggest co-occurrence of both species over a relatively small portion of the coffee plantation-border transitional habitat. Nymphal skins of these species are also mixed under *Inga* spp. trees in upland coffee, usually with 1–2 skins of each species per tree. Although my samples are small, the data suggest that *Z. smaragdula* is associated with *Zygia* trees only in the context that at both the Rosario de Grecia coffee habitat and San Ramon stream-edge habitat, nymphal skins of this species are found beneath *Zygia* trees. When *Inga* is used as a shade of upland coffee, only nymphal skins of *F. semilata* and *F. “coffea”* and *Conibosa* sp. are found near these trees, but not those of *Z. smaragdula*. Likewise, although *Fidicina*s are commonly found beneath *Inga* shade trees and even near the borders of *Zygia* with coffee, most *Zygia* habitats lack *Fidicina* nymphal skins.

The habitat complex of narrow valley strips of primary forest and adjacent patches of hillside secondary vegetation interspersed with grasslands at Es-



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parta (Fig. 5) is characterized by rather low density emergences of cicadas, some, such as *F. pronoe* and *F. spinocosta* associated with secondary vegetation and others such as *F. mannifera*, *F. sericans* and *F. amoena* associated with primary forest. In one approximately 210 m² primary forest plot containing one canopy-like *Pithecollobium* tree censused once in the dry season (10 January 1973), fresh nymphal skin abundances were: *amoena*: 20 and *sericans*: 12. A second smaller plot in the same ravine produced six nymphal skins of *sericans* and one *amoena*. The larger plot during the wet season (13 July 1974 census) produced two fresh skins of *F. mannifera* and one fresh skin of *Z. smaragdula*. Nymphal skins of *F. pronoe* and *F. spinocosta* were not searched for.

Discussion

Based on the limited data from this study, it is concluded that cicadas within the premontane-to-montane tropical moist forest zone in Costa Rica exhibit distinctive seasonal emergence patterns. Two seasonal adult emergence patterns are recognized based on my study: "dry season or tropical summer" cicadas, which include *F. semilata*, *F. "coffea,"* *F. amoena*, *F. pronoe*, *F. spinocosta*, *F. sericans*, and *Quesada gigas*, and "wet season or tropical winter" cicadas such as *F. mannifera*, *Z. smaragdula* and *Conibosa* sp. Therefore there is some evidence for allochronic annual emergence strategies in tropical cicadas within this major climatic and vegetation zone of Costa Rica, and presumably, to varying degrees, elsewhere in Central America. Extensive data on the geographical distribution of cicadas elsewhere in Central America are lacking. With the exceptions of *F. semilata* and *F. "coffea,"* all of the other cicadas studied have been observed to have the same seasonal adult emergence patterns in other major climatic and vegetation zones of Costa Rica (Young 1972, 1976, 1980a, b, 1981a; A. M. Young, unpublished data).

With the exceptions of but a few species, the genus *Fidicina* is predominantly associated with tropical dry seasons while *Zammara* with the wet seasons. *Fidicina* also represents the largest genus in Central America in terms of numbers of determined and partially-determined species, while *Zammara* is represented by two, possibly three, species based on current information. The monotypic genus *Quesada* is widely distributed in Central and South America, and also filters into the subtropical zone of North America, and it is a dry season form. Whereas the two species of *Zammara*

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Fig. 9. Collections of cicada nymphal skins over a two-year period from the three localities (lower and upper montane tropical moist forest) within the extensive coffee district northwest of the Meseta Centrale in Costa Rica. Data is for fresh skins only.

generally replace one another geographically in Costa Rica (A. M. Young, unpublished), there is considerable sympatry for the species of *Fidicina*. Because our knowledge of cicada natural history in the tropics is very meager, I hesitate to suggest that selection pressures such as competition have resulted in the evolutionary diversification and ecological differentiation of the genus *Fidicina*. Partial, tentative support of this view, however, is seen in the observed patterns of habitat partitioning in areas where several species occur together. An illustrative example would be the association of *F. pronoe* and *F. spinocosta* with secondary vegetation and the association of sympatric species such as *F. mannifera*, *F. amoena*, and *F. sericans* with primary forests. Such a pattern of ecological separation also occurs for these cicadas within the premontane tropical wet forest zone of Costa Rica (Young 1980b).

The proximal cues regulating the timing of annual emergences in tropical cicadas have not been determined and little is known about the adaptive significance of allochronic annual adult emergence patterns in these insects. Because many tropical habitats have assemblages of several species, allochrony may reduce competition for acoustical signal space, chorusing sites, and other space requirements related to reproduction. Patterns of habitat separation may be more related to resource requirements of nymphs.

Viewed within the context of ecological separation, examples of apparently microsympatric species of *Fidicina* such as *F. semilata* and *F. "coffeea"* beneath *Inga* trees in coffee plantations may have resulted from recent colonizations of these agricultural habitats when the original forest cover was cleared. Elsewhere (Young, unpublished manuscript) I have suggested that there is strong selection pressure favoring the exploitation of canopy-size Leguminosae trees in tropical forests because (a) various genera and species of Leguminosae are locally abundant in some forest habitats in different climatic and vegetational zones in Costa Rica (Holdridge et al. 1971) and elsewhere in the tropics, (b) the nymphal skins of many species of cicadas in tropical forests are very abundant beneath these trees (e.g., Young 1972, 1980a, b, 1981a; A. M. Young, unpublished) and abundances decline rapidly with increasing distance from these trees, and (c) the xylem fluids of root crowns of Leguminosae trees in tropical forests may have higher concentrations of nitrogen-containing nutrients such as amino acids than roots of other trees in the same habitats as a result of the nitrogen-fixing bacteria association with many legumes, thereby making these trees optimal feeding patches for developing cicadas. Cicada nymphs feed on xylem fluids (Cheung and Marshall 1973; White and Strehl 1978).

In a tropical region such as premontane-to-montane moist forest zone in Costa Rica northwest of the Meseta Centrale, one of the major coffee-growing districts of that country, intense removal of the forest cover and replacing it with a mosaic of coffee bushes and legume shade trees may have

allowed for the colonization of these areas by some species of cicadas already adapted for legume-feeding or to generalized legume associations in the original forest. From my observations of *Z. smaragdula* in this region and elsewhere in Costa Rica (Young 1980a; A. M. Young, unpublished), I predict that the apparent restriction of this cicada to *Zygia* trees along streams is due to sensitivity to low moisture availability in the soil rather than due to the kind of tree. Such an effect is particularly noticeable in my study from the observed distribution of *Z. smaragdula* nymphal skins near *Zygia* trees near water or low topographic points, while those of other legume-associated cicadas such as *F. semilata* and *F. "coffea"* are found with *Inga* trees on the upper slopes of coffee plantations. I doubt very much, if the legume-feeding hypothesis is correct, that *Zygia* root crowns are terribly different in terms of physical and nutritive properties from those of *Inga*, save for the difference in size (age) of the trees.

The observed densities of nymphal skins in coffee plantations for both *Fidicina* and *Zammara* falls well below densities for closely related species in relatively undisturbed forest habitats within the premontane tropical wet forest zone in Costa Rica (Young 1980b). The low densities are possibly due to the combined effects of (a) *Inga* trees, used as shade, being young or small relative to legume trees in natural forests, thereby providing less nutrients and other resources, (b) lower survival of cicada nymphs in the soil of coffee plantations and their very disturbed borders, and (c) low density courtship and oviposition by adult cicadas in the coffee plantation environment resulting from the even distribution of *Inga* trees over very large areas of the hills. Chorusing strategies in tropical cicadas are greatly influenced by the structure of the vegetation (Young 1980c, 1981b) which in turn may influence the oviposition behavior. If resources are abundant but rather uniformly distributed over large areas of habitat, the oviposition effort per resource patch may be low thereby generating low density distributions of developing cicadas.

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